The Hypopus Question, or the Life-History of certain Acarina. By A. D. MICHAEL, F.L.S., F.R.M.S.

(Read January 17, 1884.)

[PLATE XV.]

THE Acarina are so little known in this country, that it is necessary to commence by stating what a Hypopus is, and what are the questions concerning it.

In 1735 de Geer* noticed, for the first time, on the Housefly (*Musca domestica*) a tiny red mite, with an oval body enclosed in a chitinous carapace; and having, in lieu of any ordinary mouth, a minute membranous tube, apparently closed, but furnished with two setæ. The two anterior pairs of legs were thick and well-developed, but the fourth pair terminated in long setæ instead of any claw or sucker, resembling in this those of the Itch-mite (*Sarcoptes scabiei*).

Linnæust adopted the description of de Geer, and called the creature *Acarus muscarum*.

Geoffroy[‡] also found what may be presumed to be the same thing; he called it "the brown fly-mite."

Hermann§, in 1757, found upon the ventral surface and legs of a *Scarabæus* larva and the larva of *Osmoderma eremita*, a large number of small red-brown mites, with short legs and spines to the tarsi; these he called *Acarus spinitarsus*. His figure, looked at by the light of our present, somewhat wider, knowledge, leaves no doubt of the analogy between this and de Geer's species.

Schrank || in 1781 gave a description of a small mite which he found upon a male *Gamasus* (his *Acarus crassipes*), and which he called *Acarus acarorum*. This, again, is evidently an allied creature.

Dugès¶ in 1834 found, on a *Hister*, a minute mite which he regarded as being identical with Hermann's *Acarus spinitarsus*. He created the genus *Hypopus* for it, and he included in the same genus de Geer's *Acarus muscarum* and also Lyonnet's *pou*

* De Geer, vol. viii. p. 115, pl. vii. figs. 1, 2, 3.

† 'Systema Naturæ.'

t 'Histoire des Insectes,' t. ii. p. 624. no. 6.

§ 'Mémoire Aptérologique' (Strasbourg, 1804), p. 87, pl. vi. fig. 5.

|| 'Enumeratio insectorum Austriæ' (Augustæ Vindelicorum), p. 524.

¶ Ann. Sci. Nat. 2^e sér. t. i. p. 37.

de limaçon. He noticed the singular mouth with two setæ; and, in his list of genera, he put a query whether it was a larva:

Dufour^{*}, in 1839, added two species to Dugès's genus; one he found living in closely packed groups on the head and thorax of Coleoptera of the genus *Feronia*, and these he called *Hypopus feroniarum*; the other he found upon Diptera of the genus Sapromysa, and called *Hypopus sapromysarum*. He evidently regarded them as specially parasitic upon the particular creature upon which he found them; he also instituted a new genus (*Trichodactylus*) for an allied Acarid which he found parasitic upon bees of the genus Osmia.

C. L. Koch⁺, in 1843, admits the genus *Hypopus*; but in his great work he only gives one species, although, in his later work, he transfers others to the genus, one of which clearly does not belong to it. He also originated a third genus (*Homopus*) for two creatures which he found upon field-mice and squirrels, and which he at first classed among *Dermaleichi*, but which do not appear to differ materially from Dufour's *Trichodactylus*.

Dujardin[‡], also in 1843, found on the wing of a bee a small mite for which he originated a new genus (*Anætus*); this genus he subsequently suppressed, finding it to be simply a *Hypopus*.

Gervais§ next described a new species of *Hypopus*, which genus, oddly enough, he joined to *Tyroglyphus*, without having an idea of the connexion subsequently ascertained to exist, and notwithstanding the great apparent difference. It must be confessed that he also joined to it other genera which have not any connexion with it.

Dujardin || returned to the subject in 1847-1849; he then made an elaborate study of *Hypopus*, and it struck him that all the creatures mentioned above were immature forms and not species at all; it was the first time that this idea was put forward, except Dugès's query above mentioned. Dujardin called attention to the numerous ventral suckers which served the *Hypopi* as means of attaching themselves to other creatures on which

* Ann. Sci. Nat. 2e sér. t. xi. p. 278.

+ 'Deutschlands Crustaceen, Myriapoden und Arachniden': Regensburg. (In Panzer's German Insects.) 'Uebersicht des Arachnidensystems': Nürnberg, 1839–43.

‡ Ann. Sci. Nat. 3^e sér. Zool. t. ii. p. 245.

§ 'Suites à Buffon': Aptères, t. iii. p. 280.

|| Ann. Sci. Nat. 3^e sér. Zool. t. xii. pp. 243-250.

they were parasitic; he observed the absence of mandibles, and, as he considered, of any mouth whatever, and of any reproductive organs or anus. He observed that some Hypopi, immediately before the ecdysis, contained within their skin, and completely filling it, an *Acarus* different from themselves, and possessed of chelate mandibles and palpi; finding them in company with Gamasids, and in places where Gamasids were found, he came to the conclusion that Hypopus was a young form of *Gamasus*.

Fürstenberg, in 1861*, in his work on the Sarcoptidæ of Mammals, figures and describes an Acarid, which he considered as belonging to Koch's genus *Homopus*, and which Gwilt had found in immense numbers on the skin of a recently-stuffed elephant, for which, not very sufficient, reason he calls it *Homopus elephantis*. It is not quite clear why Fürstenberg deals with it at all, as he expressly says that, although a parasite, it is not an Itch-mite; probably it was because Gerlach held a different opinion and called it "Symbiotes elephantis;" but, having dealt with it, Fürstenberg gave a very different description of its mouth-organs from what other writers had given for *Hypopus*; he described maxillæ divided into two equal parts and placed between three-jointed palpi. Fürstenberg carried his measurements to the 4th place of decimals of a millimeter.

Claparède⁺ was the next contributor to the literature of Hypopus, in the year 1868; he may certainly have the credit of first connecting Hypopus in an intelligent manner with Tyroglyphus, although Gervais had classed them together. Claparède found, on hyacinth-bulbs, &c., what he considered to be a new species of Tyroglyphus. He had it in great profusion, kept up his observations for three years, and bred large numbers of the creatures. which he called Tyroglyphus Dujardinii; but he never found a male, all the specimens he noticed were females. He did not find any Gamasids, but he did find great quantities of Hypopi, and moreover he actually saw some nymphs of Tyroglyphus, which closely resemble the adult, cast the skin and produce, not a perfect Tyroglyphus, as the other nymphs of the same species did, but a Hypopus. He never could see any eggs in a Hypopus. Claparède's observations were absolutely correct, but the deduction which he drew from them was that Hypopus was the male of Tyroglyphus. Claparède took the opportunity of attacking

* 'Die Krätzmilben von Menschen und Thieren' (Leipzig, 1861), p. 208.

† "Studien an Acariden," Zeitschr. wiss. Zool. 18 Band, p. 445.

Fürstenberg's *Homopus*, which he declares to be wrongly described, and to be an ordinary *Hypopus*.

Claparède's suggestion that Hypopus was the male of Tyro-glyphus was practically disproved before he made it, for, while Claparède was studying this Tyroglyphus, he was not aware that Professor C. Robin and Dr. Fumose were doing the same thing; they published their paper* shortly before Claparède's. They called the species T. echinopsis, which name must stand. They did not deal with Hypopus, which they apparently did not trace as being connected with the life-history, but they did find the unquestionable male of the species.

P. Mégnin took up the subject in 1873, first in his memoir upon $Tyroglyphus rostro-servatus^{\dagger}$, and afterwards in his memoir on $Hypopus^{\dagger}_{\pm}$; and his labours were rewarded by the French Académie des Sciences with the Thoré Prize of 1873. His may be said to be the present theory.

Mégnin experimented upon Tyroglyphus rostro-serratus and T. mycophagus, both of them species found by him in immense quantities on mushrooms (Agaricus campestris); he bred his creatures in cases, supplying them with pieces of fresh mushroom from time to time. He found that when the mushrooms and cages got dry, his Tyroglyphi disappeared, and were replaced by swarms of Hypopi; when moisture was added, the Hypopi disappeared, and the Tyroglyphi were again in great quantities. Specimens which he kept in separate cells appeared to be almost inert, and adhered motionless to the side of the cell, but when moisture was added, these Hypopi turned into nymphs of Tyroaluphus. The construction which Mégnin put upon these facts is, that Hypopus is a form into which nymphs of Tyroglyphus change, when, through dryness of the atmosphere, or other causes, there is a difficulty in their continuing to live as Tyroglyphi, and that it is a provision of nature to insure the preservation of the species, by carrying it over periods of drought, &c.; he also saw the Hypopus inside the nymph of Tyroglyphus just before the ecdysis, as Claparède had done.

Mégnin also attacks Fürstenberg-declares that the latter's mouth-organs were pure fancy, and speaks very strongly against

^{*} Journ. de l'Anat. et de la Physiol. (Robin's), 1868, No. 3 (May and June).

 $[\]dagger$ Comptes Rendus Acad. Sc. Nat. 1873, 2° sér. pp. 129 and 492; Journ. de l'Anat. et de la Physiol. (Robin's), t. ix. p. 369 (1873).

[‡] Ibid. t. x. p. 226 (1874).

such exercises of imagination. He regards *Hypopus*, *Homopus*, and *Trichodactylus* as being all similar things, and as having the power of remaining without any nourishment during the whole period of their existence in this stage, and this view he supports in a special paper on the subject^{*}.

In a subsequent memoir[†], Mégnin extends his view of the nymphs of certain *Acarina* assuming a hypopial condition in order to preserve the species under adverse circumstances, so as to include the case of certain *Acari* found in the cellular tissue of birds by Giuseppe Gené[‡], Charles Robertson[§], Montagu^{||}, and Filippo de Filippi[¶], which the last-named writer called *Hypodectes*, but which Mégnin considers to be the hypopial nymphs of feather-feeding Sarcoptidæ (*Pterolichus falciger*).

In one of his latest works^{**} Mégnin states that Dufour's Hypopus feroniarum is the hypopial nymph of Tyroglyphus rostro-serratus (Serrator amphibius), Mégnin, and that the Acarus spinitarsus of Hermann is the same as Homopus elephantis, Fürstenberg, and is the hypopial nymph of the common Cheese-Mite (Tyroglyphus siro). He does not say how the last fact was ascertained; and in his memoir on Hypopus, above quoted, he states Hermann's spinitarsus to be the hypopial nymph of his Tyroglyphus mycophagus.

Mr. Tatem^{††}, in 1872, figured and described, under the name of *Acarellus muscæ*, a creature which is a *Hypopus*, and which he is of opinion that he took from the abdominal cavity of a dead flea.

Andrew Murray^{‡‡}, in November 1876, entered vigorously into the dispute. He does not seem to have made any personal observations, but he elaborately discusses almost all the above-

* "Mém. sur les Hypopes," Journ. de l'Anat. et de la Physiol. (Robin's), t. x. p. 225 (1874).

† "Les Acariens parasites du tissu cellulaire, &c., des Oiseaux," ibid. t. xv. p. 120 (1879).

‡ 'Brevi cenni su un Acaridio del genere dei Sarcopti che vive sulla Strix flammea:' Torino, 1848.

§ Microscopical Journal, Feb. 1866.

|| Mem. Wernerian Nat. Hist. Soc. 1808, vol. i. p. 176.

¶ "Note zoologiche 1. Hypodectes nuovo genere di Acaridi," in Archiv per la Zool., l'Anat. e la Fisiol. fasc. i. pp. 54-60: Genova, 1861.

** 'Les parasites et les maladies parasitaires ': Paris, 1880.

+ Monthly Microse. Journ. 1872, p. 263, pl. xl.

tt 'Economic Entomology, Aptera': London, 1877.

named authorities, and finally comes to a totally new conclusion, viz., that *Hypopus* is a ferocious predatory parasite, and that it eats its way into the body of its victim, and then devours its whole internal parts, only leaving the skin. He quotes the example of *Rhipiphorus paradoxus*, to show that a creature may be an external parasite at one period of its life, and an internal one at another.

Notwithstanding Mégnin's exposition, some acarologists of emineuce continued to consider Hypopus as a separate adult creature, and continued to frame new species and genera for newly discovered hypopial forms. Profs. G. Canestrini and E. F. Fanzago's Chironemus*-afterwards changed to Tarsonemust, because the former word had been already employed for a genus of fishes-consists of Hypopi. Dr. P. Kramer's female Dendroptust appears to be the same thing. Canestrini and Fanzago also preserve Dufour's genus Trichodactylus§. The Labidophorus talpa of Kramer also appears to be a hypopial form ||. In the last-named paper Kramer also described another very singular parasite of the Mole, which he called Pygmephorus spinosus, which has an immensely developed monodactyle claw to the front leg, and somewhat rudimentary mouth-organs; he described the male only. R. Canestrini subsequently added a new species, mesembrinæ¶, to Kramer's genus Pyqmephorus.

G. Haller, in 1880, published a paper^{**} upon Acarina parasitic upon Invertebrata, in which is a summary of existing writings on the subject, and in which, although he does not record any special observations of his own upon the point, he suggests that the hypopial form is a "travelling-dress" for *Tyroglyphus*, to enable it to endure the journey from one fungus, &c., to another, which would sooner or later be rendered necessary by the drying or destruction of the fungus.

* "Nuovi acari Italiani," Atti Soc. Veneto-Trentina di Sci. Nat. vol. v. fasc. i.

† "Nuovi acari Italiani," ser. 2, ibid.

t "Ueber Dendroptus," Archiv für Naturg. xlii. Jahrg. (1876), p. 198.

§ "Intorno agli acari Italiani," Atti R. Ist. Veneto di sci., lett. ed arti, ser. 5, vol. iv. p. 137.

|| "Zwei parasitische Milben des Maulwurfs," Archiv für Naturg. xliii. Jahrg. (1877), p. 248.

¶ "Contribuzione allo studio degli acari parasiti degli insetti," Atti Soc. Ven.-Trent. di Sci. Nat. vol. vii. fasc. ii. (1881).

** 'Die Milben als Parasiten der Wirbellosen :' Halle, 1880.

Finally, in 1881, A. Berlese published a paper* in which he in the main agreed with Mégnin, but went somewhat further, asserting that Kramer's *Pygmephorus* was not an adult form, that *Hypopus* took no nourishment, and was entirely without buccal or anal apertures, that its labium was a tactile organ, and that all *Acarina* which had rudimentary mouth-organs, and were without buccal and anal openings, were hypopial forms. This paper is complicated by the author's exceptional views as to polymorphism, &c.

These are the principal records; but Mr. J. S. Macintyre informed me that he also has seen *Tyroglyphi* turn into *Hypopi*, although I am not aware that he has published his observations.

I have not attempted an exhaustive abstract of any of the above-named papers, many of which are lengthy, but have simply sought to set out, in as few words as possible, such parts as are essential to an understanding of the aim and results of my own observations; and also, to some extent, to draw attention to what has been done by others. To summarize the literature, eight different suggestions are before the public as to what a *Hypopus* really is; these are made by the writers whose names are set opposite to the respective explanations, viz. :--

1.	Hypopus is a separate family of adult Acarina	Writers before Dugès ; also Koch, Dufour, and some pre- sent authors.
2	Hypopus is an immature stage of Gamasus	Dujardin.
3.	Hypopus is an itch-mite	Gerlach.
4.	Hypopus is the adult of both sexes of some)	Gervais.
5.	Hyponus is the male of Tyroglyphus	Claparède.
6.	Hypopus is the "cuirassed heteromorphous adven- titious nymph of Tyroglyphus," &c., appearing only (for the distribution and preservation of the species (under adverse circumstances	Mégnin, Berlese, &c.
7.	Hypopus is a ferocious parasite, sometimes ex- ternal, sometimes internal, which ends by entirely devouring its host from within, leaving only the skin	- Andrew Murray.
8.	Hypopial form is a travelling dress	Haller.

It is the correctness or error of these diverse opinions that I

* "Indagini sulle Metamorfosi di alcuni acari insetticoli," Atti R. Ist. Veneto di sci., lett. ed arti, ser. 5, vol. viii. have endeavoured to ascertain; but first let me say a few words as to what a *Hypopus* is like.

There are several forms of Hypopus, differing more or less from each other, but to take a typical kind, such as Dufour's feroniarum, it is an extremely minute Acarid, rarely more than 25 millim. in extreme length, which presents, at first sight, somewhat the appearance of a miniature Limulus without a telson, its whole dorsal aspect being entirely covered by a nearly hemispherical, chitinous carapace, concealing cephalothorax and abdomen, and coming to the ground all round when the creature is quiet. The two front pairs of legs and the long setæ at the ends of the fourth pair project somewhat when the animal is walking, but can be entirely withdrawn under the carapace, and usually are so. The mouth-organs are very rudimentary, consisting, it is asserted, of a mere hole, covered and closed by a flap, and from which projects a tube of moderate length, getting finer towards the distal end, where it is said to be closed, and which tube terminates in two long bristles, which do not pass within the tube, and cannot, it is said, be regarded as maxillæ. The ventral surface is covered with a soft integument, and bears numerous suckers, chiefly near the posterior part; by these suckers the creature adheres to the polished, chitinous surfaces of Insects. Gamasids. &c.

The three front pairs of legs terminate in a double claw, and caruncle or sucker; the fourth is without either, and terminates in very long bristles, like the hind legs of *Sarcoptes scabiei*, but larger in proportion; this is probably what deceived Gerlach, and led him to consider it an Itch-mite. The chitinous carapace is frequently sufficiently transparent to allow the form of the creature to be seen through it.

For some two or three years I had carefully watched *Tyro-glyphi* in confinement in small glass cages, under favourable and unfavourable conditions, but my efforts were chiefly directed to *Tyroglyphus siro* and *longior*, and I did not succeed in getting any hypopial forms from them, nor in seeing any thing that would elucidate the question. In 1881, however, I came across a quantity of Mégnin's *Tyroglyphus mycophagus*; I soon found that, with this species, there was not any difficulty whatever in repeating his experiments. The nymphs readily turned into *Hypopi*, and the *Hypopi* returned to the form of nymphs of the *Tyroglyphus*, in each case by an ecdysis; and I was able to secure

and preserve microscopical slides, mounted during the progress of the change, and showing the Hypopus forming, or formed, inside the Tyroqlyphus nymph, which I still possess. This appears to be sufficient to answer Andrew Murray's view that Hypopus is an internal parasite; because, firstly, the Hypopus is very nearly as large as the Tyroglyphus from which it emerges, filling up the whole interior, which seems highly improbable with a creature which cannot grow inside; for we never see young Hypopi smaller than their fellows either within the Tyroglyphus or living free. All the Hypopi of the same sort which are found are about the same size. Secondly, we never, by any chance, see a Hypopus within the larva or within the adult, only within the nymph; although the difference between larva, nymph, and adult in Tyroglyphus is very slight. Thirdly, we never see two Hypopi within the same Tyroglyphus, although, when the Hypopus has emerged. we often find numbers ectoparasitic upon the same Gamasus, insect, &c. Fourthly, the emerging of the Hypopi is preceded by an inert period, just as the ecdysis is in most Acarina. Fifthly, the Hypopus, when it emerges after the ecdysis, leaves behind it the cast skin quite clean, and without any torn particles of internal organs adhering to it; in fact, in the ordinary state of the exuvia of Acarina and insects. Sixthly, the mouthorgans of Hypopus are not in any way fitted to consume the solid tissues of its host. Seventhly, the Hypopus returns to the Tyroglyphus-form after the next ecdysis.

If these considerations dispose of Andrew Murray's suggestion, as I think they do, they also dispose of the view that *Hypopus* is a distinct creature; for that could now only be sustained if Murray's view were received; otherwise the evidence of Claparède, Mégnin, Berlese, Macintyre, and myself, who have all actually seen the change, would probably be accepted as sufficient to prove that the form is a stage in the life-history of *Tyroglyphus*.

Claparède's view, that *Hypopus* is the adult male, was practically answered by Robin and Fumose; and it will, I think, be found below that it is even more effectually disposed of by my own observations in 1882, which would also answer Gervais's idea. There therefore only remain Mégnin's and Haller's explanations. My observations decidedly confirmed Mégnin's view, that the true *Hypopus* is a heteromorphous nymphal form of *Tyroglyphus*, and possibly of some allied, or other, genera.

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It remained to be seen whether I should be able to verify his conclusions as to the causes of the transformation. For this purpese I allowed the cell to get dry, but I did not thereby obtain any increase in the number of *Hypopi*; although I did find a very great diminution in the number of *Tyroglyphi*, which died off, as the moisture became insufficient, until they disappeared altogether. Upon redamping the cell more larvæ and young nymphs soon made their appearance from the eggs which the previous adults had laid, and older nymphs from the *Hypopi* were found undergoing ecdysis; but this occurred gradually, not all at once: the *Hypopi* did not vanish suddenly, nor were fresh adults to be found until they had grown. It must be remembered that I did not introduce fresh fungus into my cells as Mégnin did.

This experiment of allowing the cells to dry, or partially dry, was repeated several times, but always, practically, with the same results. It would seem, therefore, that desiccation or other unfavourable circumstances, will not necessarily cause *Tyroglyphus* nymphs to change into *Hypopi* more rapidly than they would otherwise have done.

In the spring of 1882 I resumed the subject. I was staying at a farm-house where they had an old-fashioned chaff-house adjoining the stable: this was not kept in the well-swept condition usual in modern stables, but the chaff and debris of the fodder were allowed to remain in a pile on the brick floor, which was always rather damp, and altogether the conditions were as favourable to Tyroglyphus life as can well be imaginedwarmth, moisture, and abundant food were there, and, consequently, the chaff was teeming with life; Tyroglyphi were swarming, Gamasids were there in quantities preying upon them, and minute Diptera and their larvæ, Myriapoda, &c., were abundant ; but Hypopi also were in great profusion, and continued to be so. and to attach themselves to every living insect or Gamasid which came into the chaff. It was evident, therefore, that the most favourable circumstances did not prevent the Tyroglyphus becoming a Hypopus. The principal species of Tyroglyphus were T. farina, T. mycophagus, and Mégnin's T. rostro-serratus (subsequently called Servator amphibius by him, Phyllostoma pectineum by Kramer*, and Histiostoma pectineum by Cauestrini and Berlese[†]).

* "Beiträge zur Naturgeschichte der Milben," Archiv für Naturgesch. xlii. Jahrg. 1876, p. 39.

† "Nuovi acari," Atti Soc. Ven.-Trent di Sci. nat., vol. viii. 1881.

The hot-bed for cucumbers at the same place, which was made up from the stable-manure, and which presented equally favourable conditions, swarmed with *Hypopi*, which covered every small dipterous insect that emerged from the hot-bed.

I now endeavoured again to try the converse experiment. Ι collected a number of Tyroglyphi and placed them in two kinds of glass cells, viz .: -1, the small cells which I use for breeding Oribatidæ, which are covered up by a glass plate, and in each of which I only put one or two specimens, so that I can watch and know each individual; 2, the other, the larger cells (small dissecting troughs), which I use for breeding Gamasida, where the cover is pierced with a few small holes, with muslin over them, so placed that they can be made to communicate with the interior of the cell or not as desired, by moving the cover : in these cells a number of specimens can be placed if it be wished. I now tried similar cells, each with a number of Tyroglyphidæ, and, when they were breeding freely, allowed one cell to get dry and kept the other in proper hygrometric condition. I did not find that I got more Hypopi in the cell that dried than the other; on the contrary, I got more Hypopi where breeding was under favourable circumstances, and, consequently young nymphs more abundant; but I did find that as the cell dried the Tyroglyphidæ retired into any hole or shelter which afforded a prospect of retaining moisture. Thus I kept a small piece of blotting-paper in the cell in order to damp when more moisture was required, for actual water must not be put in in drops on the glass, or the Acari will drown. As the cell dried, I sometimes found that the Turoglyphi all got under the blotting-paper, and I could not see one of them; but if the drying process were stopped short of what would destroy life, and fresh moisture added, they soon came out again; if fresh moisture were not added they died, and were not seen again. The Hypopi endured drought better, but if it were continued, they died also. I repeated these experiments several times, but always with the same result. This may possibly account for the way in which Mégnin's Tyroglyphi disappeared and Hypopi appeared when the cell got dry, and the former reappeared on adding fresh fungus, in his glass cages containing strips of fungus. However that may be, I did not succeed in producing or hastening the change to Hypopus by drying. either in the larger cells, or in the smaller where I could watch the individual Acarus.

At this time *Hypopi* were numerous in moss in the neighbourhood. In April (1882) I took two similar specimens from moss, and placed them alone in a small glass cell with blotting-paper. In a few days they became inert, and one changed into a *Tyroglyphus* nymph, leaving its exuvium on the blotting-paper. The other soon afterwards did the same. Early in May one of the nymphs underwent ecdysis, and became an adult *Tyroglyphus*; about the 13th of May the second became inert, and shortly afterwards changed to an adult *Tyroglyphus*.

One thing that became evident in breeding the *Tyroglyphi* and *Hypopi* was that the full-grown nymphs of the former did not change into the latter, but that it was the young nymphs that changed, and that the change occurred always at the same stage of the life-history. It appeared to me, with those species which I have observed, that the change occurred at the second nymphal ecdysis, and the hypopial form continued until the following ecdysis: this probably accounts for the small size of the *Hypopus* compared with the adult *Tyroglyphus*.

I found, by carefully watching individual specimens, that they do not all turn into *Hypopi* during the course of their life-history, but, on the contrary, most proceed from larva to nymph, and through all the nymphal ecdyses, and become adult, without assuming a hypopial condition; but that, whatever be the conditions under which they are kept, *Hypopi* will keep appearing if the species be one where the *Hypopus* is easy to breed, and if young nymphs be present.

Another matter which I was careful to watch, was whether both sexes or only one assumed the hypopial form, as it might be possible that, although Claparède was wrong about their being adult males, they still might be a form confined to one sex. I therefore watched this in cells into which I had put several *Hypopi*, but not any other Acarina nor ova. I found that the *Tyroglyphi* which emerged from the hypopial skins were of both sexes; the female predominated, but not more than it usually does in *Acarina*.

What, then, is the reason of this hypopial stage? It seems to me that it is simply to facilitate the distribution of the species, so that the *Acarus* may lay hold of any small living object that comes within its reach, and be carried to "fresh fields and pastures new," which it could not otherwise reach. It is manifest that, being carried by such creatures as bees, flies, &c., which delight in hot sunshine, a thing which kills most *Acari*, the hypopial condition, which enables this creature to endure greater heat and absence of moisture than the ordinary *Tyroglyphus*-form can survive, must be of advantage to it.

It may be worth consideration whether the travelling of Hypopi may not be the explanation of Tyroglyphidæ appearing suddenly in places where they have not appeared before, and where their presence is not desired or its cause understood, a matter very troublesome occasionally in a household. A fly or a bee would not be suspected, and may convey a few small, almost invisible Hypopi, which would soon become adult, and then multiply with great rapidity. Another instance may be the frequent appearance of mites (Tyrogly phus entomologicus) in collections of insects; two or three specimens, if they became adult, would soon produce a quantity of Tyroglyphi, which would greatly injure the entomological preparations, and these two or three specimens might often be adhering to the insects in the collection when introduced, and pass unnoticed, being concealed by hairs &c. Hypopi often remain a long time in that condition; I have had them over three months.

It now remains to consider Dufour's *Trichodactylus*. It has been mentioned above that, n 1839, this naturalist instituted a genus, thus named, for a creature resembling *Hypopus*, which he found on bees of the genus *Osmia*. Dufour's figure and description show the regular *Hypopus* rostrum and the first three pairs of legs, similar to each other, somewhat long, of nearly equal thickness throughout, and terminated by a long, slightly curved, double claw. The fourth pair of legs are clawless, and terminate in long setæ in the true *Hypopus* fashion. Dufour's figure and description are rather slight.

In 1875 Prof. A. L. Donnadieu published * an elaborate and careful treatise upon this species (as he considered) and on an Acarid found by him upon *Xylocopa violacea*, which he names *Trichodactylus Xylocopiæ*. These creatures have the fourth leg terminated by one or three very long setæ, according to species, in the *Hypopus* manner, like Dufour's *Trichodactylus*. In Donnadieu's specimens, however, the first leg is much thicker than the others, and is terminated by a very large and remarkable *single* claw, apparently formed for holding hairs, and greatly resembling

* "Recherches anatomique et zoologique sur le genre Trichodactyle," Ann. Sci. Nat. 5° sér. Zool, t. x. pp. 69-85. the claw of *Pediculus capitis*. The second and third legs are also terminated by single claws, but less remarkable in size and form. Donnadieu says that Dufour has confounded the two species, and that, probably from the imperfection of his instruments, he has misdescribed the creatures in many respects, and in particular as to the legs, where, in addition to other errors, he has described double claws instead of single. Donnadieu's Acarids had a soft closely-wrinkled skin resembling *Sarcoptes*, to which genus he considers *Trichodactylus* to be allied, although it is not subcutaneous. Donnadieu describes both sexes, and gives details of the reproductive organs and of the mode of copulation: he describes the maxillæ, mandibles, lingua, &c., and gives excellent drawings of the whole.

Dujardin considered that Dufour's Trichodactylus was the same as Hypopus, and, in spite of Donnadieu's details, Mégnin, Berlese, and others have maintained that the two so-called genera are identical, and that consequently Trichodactylus consists of immature forms, and not of species at all. I am not inclined to offer an opinion as to what Dufour's species is upon the evidence of his paper alone; but I am indebted to the kindness of Prof. Donnadieu for the loan of the only two specimens of his two species which he still possesses, and the examination of them has decidedly led me to the conclusion that they are not Hupopi, but are adult creatures, and that, as far as I can judge, Donnadieu is right in considering them to be somewhat allied to Sarcoptes. Whether they be identical with Dufour's species seems to me a more doubtful question. I may mention that Donnadieu's species are very much larger than any Hypopi which I have ever seen. I did not receive them or come to the conclusion that they were good species, until after I had had the advantage of making the investigations referred to below upon Mr. George's bee-parasites.

In April 1879, Mr. C. F. George, of Kirton Lindsey, published a short account of an Acavid which he found the previous year parasitic upon the Gamasidæ which were infesting the Queen humblebees, particularly *Bombus virginalis*^{*}; he says he "supposes it must be a *Hypopus* (whatever that may be)." The whole of the cephalothorax of this creature, which is far the largest portion of it, is covered by a polished, chitinous carapace, extending greatly

* "On the Mite of the Humble-Bee, Gamasus," Science Gossip, vol. xv. pp. 81, 82 (1879).

beyond the body (Pl. XV. figs. 3-4); the abdomen, however, projects behind this carapace, and is decidedly segmented, a most exceptional thing in adult Acarina, although sometimes found in larvæ. The first leg is much enlarged, and is provided with a great, single, holding-claw, exactly like Donnadieu's *Trichodactylus Xylocopiæ*, but, oddly enough, the second and third legs have didactyle claws, like Dufour's figure, which was considered an error. The fourth leg is terminated by long setæ, as in *Hypopus*, *Trichodactylus*, &c.

When this account appeared I, like its discoverer, imagined it to be a *Hypopus*, and I have ever since been desirous of investigating its life-history, greatly with the view of assisting to decide the *Hypopus* question. It was not, however, until the spring of the present year (1883) that I succeeded in obtaining healthy living specimens in sufficient numbers to enable me to carry out the research. This year, however, partly from my own captures of humble-bees, and partly from the supplies of living specimens sent me by that excellent collector Mr. E. Bostock, of Stone, I found myself in a position to pursue the subject.

Mr. George apparently regarded his so-called Hypopus as strictly a parasite of the *Gamasus* which lived on the bee, not as a parasite of the bee itself. I, however, soon found, when I had an ample supply of material, that quite as many existed on the bee as on the *Gamasus*: my first hope therefore was that I might keep the bee alive with the whole united-happy-family of *Gamasidæ*, *Hypopi*, &c. I was unfortunately entirely unable to do so under any conditions which would enable me to watch such small creatures as the *Hypopi*; I therefore had to abandon this idea, and limit my ambition to keeping alive such Gamasids as bore *Hypopi*, which I knew that I could do. In the meantime, however, I had found several solitary specimens of the supposed *Hypopus* in moss, where I was searching for Oribatidæ; these were not parasitic upon any thing, and it therefore struck me that possibly the *Hypopi* might live in a cell without any host.

tried, and found that they lived very well for a considerable time; and, as hereinafter stated, I ultimately found that, when I had discovered suitable food, they lived quite as well without any host as with one. I did not employ any of the *Hypopi* found in moss for my investigations, for fear of confusion of species, but confined myself strictly to those found on the bee or on the Gamasidæ infesting it.

Having got my creatures to live, the next step was to watch the life-history, and observe what this particular Hypopus turned into. I expected to see it turn into Tyroglyphus, and I started several cells with living Hypopi, the cells being divided into three series, differently treated. In series 1 I put only Hypopi which were on the bee itself; in series 2 only Gamasids bearing Hupopi: in series 3 both separate Hupopi (as in series 1) and Gamasids (as in series 2). I placed my captures under what seemed to me the most favourable circumstances; but, to my annovance, they obstinately refused to turn into any thing ; they lived a considerable time, were tolerably active, but eventually died, and no information was obtained : this was specially true of series 1. As to series 2 I found that the Hypopi which I had put in loose soon got on to the Gamasids, occasionally as many as six upon one Gamasid; but in the same series, and in number 3, I also found the converse, viz. that the Hypopi gradually left the Gamasids and wandered about loose. I now became afraid that if the Hupopi turned into Tyroglyphi, or any thing similar, the Gamasids would eat the adults and I should not see them ; therefore I gradually removed from some of the cells the Gamasids which no longer bore any Hypopi. Another source of difficulty existed with those cells which contained Gamasids ; in order to keep these Acarids in health I have found it best to feed them on cheese-mites (Tyroglyphus siro), as I do not know any equally suitable living food which can be procured so easily. I thought I should be sure to know T. siro from any thing that the Hypopi might turn into; but it was possible they might be so alike that I might not distinguish them. Regularly feeding the Gamasids with cheese-mites is rather laborious; so in one cell I tried the effect of putting in a minute scrap of cheese for the cheese-mites to breed in. Coming to examine this cell on 22nd April, 1883, I found, to my surprise, that all the Hypopi had left the Gamasids and were grouped together on the cheese. I removed the Gamasids, and then gently lifted some of the Hypopi off the cheese. I found below them a number of almost globular, milkywhite eggs, which struck me immediately as being different from cheese-mites' eggs. Of course the supposition immediately presented itself that the supposed Hypopi were not Hypopi at all, but were adult creatures, and had laid these eggs. This, however, required a good deal of confirmation. I removed the eggs and placed them in a separate cell, without any other Acari. T

examined this cell on the 28th April, and found that the eggs had mostly hatched, and that the cell contained a number of hexapod larvæ which were unknown to me: all the three legs had didactyle claws. This creature is described below and is figured at Pl. XV. fig. 1. These larvæ grew rapidly, and on the 1st May I found that some had become inert and had swollen up into mere shapeless lumps, as is common with the Acarina before the ecdysis. I expected to see an octopod nymph emerge from this inert creature, but on the following day (May 2nd) two socalled Hypopi, exactly like those caught on the bee, emerged from the inert larvæ, and more subsequently emerged. I found, however, that some, when they emerged, were very different from the supposed Hypopi, and were not creatures enclosed in a hard carapace any more than the larvæ had been. This puzzled me, as it appeared as if it must be the nymph, and as if I had missed that stage in the other specimens *. From what I subsequently observed, however, the supposed nymphs appear to be the males, although so very different from the females as not to be suspected at first. This male is described below, and figured, Pl. XV. fig. 2.

This creature has the posterior part of the abdomen covered by a brown shield-shaped plate, which makes it very conspicuous amongst the larvæ; it also has the hind legs very thick and peculiar in form, but they are terminated by setæ, not claws nor suckers. It is smaller than the adult female, and even than the larva in its final inert, swollen condition. While I imagined this to be the nymph I put several specimens, in many instances, into separate cells, hoping to see them change into adults. Nothing of the kind, however, took place; they lived for some time, and then died, but without change. In the meantime, however, I began to observe that, among those which had not been separated, one of these supposed nymphs, with the brown abdominal plate, was frequently attached to a white inert larva, the singular hind legs of the nymph grasping the larva, which the nymph dragged about with it wherever it went. At last this became so general that there was hardly an inert larva in the cells that was not in the possession of one of the brown-tailed forms. These facts, taken together, naturally led me to the conclusion that I had probably really got the male, not the nymph; and an examination

 $\ast\,$ This appeared more probable, as the nymphal stage occurs in almost all other Acarina with which I am acquainted.

with a view of ascertaining this soon led to the discovery of a comparatively large, chitinous organ, below the brown shieldshaped plate, which closely resembles the penis in many species of Sarcoptidæ parasitie on birds, as, for instance, *Proctophyllodes* glandarinus, which are the very creatures where a similarity might be expected to occur. I feel no doubt, therefore, that this is the male; but, from the varying position in which the inert larva is held, I do not look upon the process as actual coition, but rather as a holding possession with a view to coition immediately the adult female should emerge, possibly before the chitinous carapace had time to harden. I do not, in this, rely on the fact of the inert form being immature; as in the above-named case of *P. glandarinus*, and in other members of the Analginæ (Dermaleichi), the male always copulates with a female which has not undergone the last ecdysis nor assumed its final form.

The inert larva, when it is dragged about by the male, generally has the wholly or partly formed adult female showing plainly through the semitransparent larval cuticle.

I had observed that the cheese vanished slowly, even in those cells which did not contain any cheese-mites, and that what I will, for the moment, still call the *Hypopi*, for want of a better name, were very much about it. I therefore afterwards tried it in breeding, and found that they throve well where it was. Utilizing this, I placed some of those which I had just bred from the eggs into a separate cell, and I succeeded in getting them to lay eggs, and in rearing these eggs through their whole life-history, as I had done in the first instance; and this I repeated through several generations, always with the same results, and without the assistance of any bee or *Gamasus*.

I have never seen either the larva or the male upon the bee or the *Gamasus*, only the adult females; this is not altogether exceptional among *Acarina*, as in many Gamasidæ the females and nymphs are parasitic, either temporarily or permanently, although the male never is so.

I think that the above detailed experiments prove that this socalled *Hypopus* of the *Gamasus* of the humble-bee is a separate adult species, fairly forming the type of a distinct genus. I propose to call it "*Disparipes bombi*" *.

* Decidedly the nearest ally is Kramer's *Pygmephorus*: the rostrum, body, and a large portion of the general arrangement is strikingly similar, but the great difference in the fourth pair of legs, the absence in *Pygmephorus* of the chitiI believe that it will be found that this is not a single species, but is rather the type of a considerable genus. I have found a number of females closely resembling those of D. bombi, but so very much smaller that they can scarcely be the same, as intermediate sizes do not occur. I have also found in moss a very small species which appears to have the adult female, male, and larva, which is dragged about by the male, all having a sufficient similarity to D. bombi to justify their being included in the same genus. The adults are usually of a bright green colour, somewhat varied occasionally with yellow and black, the colour being greatly communicated by the food. I hope to describe this more fully on a future occasion, and in the meantime would call it provisionally *Disparipes viridis*. I have also found other creatures which will, I think, have to be allotted to the same genus.

To summarize the results of my observations, it appears to me:---

1. That true *Hypopi* are not adult animals, but are a stage in a life-history.

2. That they are heteromorphous nymphs of *Tyroglyphus* and some allied genera.

3. That it is not all individuals that become Hypopi, but only a few.

4. That the hypopial period takes the place of that between two ecdyses in the ordinary life-history.

5. That, in those species which I have examined, the hypopial stage commences with the second nymphal ecdysis.

6. That the change to *Hypopus* is not caused by unfavourable circumstances, and is not any extraordinary or exceptional circumstance, but is a provision of nature for the distribution of the species occurring irrespective of adverse conditions.

7. That, in the present state of our knowledge, we can no more say why one nymph becomes a *Hypopus* and another does not, than we can say why one ovum produces a male and another a female.

8. That *Hypopi* are not truly parasitic, but only attach themselves to insects, &c., for the sake of conveyance, and that they do not confine themselves to any particular insect, but adhere to any suitable moving object.

nous hood covering the front part of the body of the female, and other things would, I think, prevent both species being properly included in one genus. I think Berlese was in error in considering *Pygmephorus* to be an immature form. 9. That the external form of *Hypopus* is a protective provision given to some *Acarina* which have to be distributed by attaching themselves to insects or other creatures, which will expose them to heat and draught that would kill them, were it not for this protection; and that the protective dress may be given either to immature or adult creatures.

10. That the creature which I have called *Disparipes bombi* is an adult aud a separate species of which the females only have assumed what may be called the hypopial dress, and are parasitic, probably as a means of conveyance.

11. That there appear to be other species of the same genus.

12. That probably Donnadieu's bee-parasites are adult species as he says, but that it is not absolutely certain that they are identical with Dufour's *Trichodactylus*.

Order ACARINA.

Suborder TRACHEATA.

Family MYOBIADÆ.

Genus DISPARIPES.

Characteristics of the Genus.—Legs dissimilar. First leg terminated by a single claw, without caruncle, and second and third legs by a double claw, with or without a caruncle, in both sexes. Fourth legs much thickened, terminated by very long setæ without claw or caruncle; setæ different in the two sexes. Anterior part of female entirely hidden beneath a chitinous carapace. Rostrum articulated to cephalothorax, and bearing four rod-like projections; other mouth-organs rudimentary, or very slightly developed.

DISPARIPES BOMBI, gen. nov. Plate XV.

Male (fig. 1). Average length, about '22 mm,

,,	breadth, about '12 mm.		
,,	length	of legs,	1st pair, ·11 mm.
• •	,,	,,	2nd pair, ·10 mm.
		,,	3rd pair, 11 mm.
>>	,,	"	4th pair, '07 mm.

Colour semitransparent white, with a yellowish shade in parts. A large shield-shaped space at the posterior end of the notogaster brown. The excretory organs show through the dorsal surface, forming a large, opaque, white mark.

Texture rough and leathery, not hard nor chitinous.

General form an elongated diamond, with curved sides.

Cephalothorax and abdomen. Rostrum very small and colourless, articulated with the cephalothorax; sides almost parallel; two short rod-like or tubular projections from the anterior border of the rostrum, and two similar, but rather larger, inserted in a notch in the side of the rostrum, like palpi. No demarcation between cephalothorax and abdomen; hinder portion of notogaster covered by a brown, chitinous, shield-shaped plate, not quite coming to the edge of the abdomen; the soft parts outside the plate ragged in outline and bearing a few short, clear spines. Notogaster bearing four rows of very large serrated spines. No part of the creature covered by any carapace.

Legs of 5 free joints; there is also a large basal portion which may be an epimeron, or may be equivalent to a fixed coxa. First pair articulated to the anterior margin, gradually diminished in thickness towards the distal extremity; every joint bears one or more whorls of large spines; there are several on the tarsi; which are terminated by small single claws on long straight peduncles, with a very large serrated seta above it and another nearly opposite. Second and third legs articulated at the side of the body, slightly below; somewhat similar in shape to the first pair, but tarsi more curved, and terminated by a didactyle claw, with caruncle; set a smaller than those of the first leg, but the penultimate joint of the second leg bears a curious curved chitinous projection on the outside and a strongly pectinated seta on the inside. Fourth legs short, but very thick, curved inward, ending bluntly; no claw nor caruncle, but two long setæ not quite terminal, the upper one being the longer. There is a large spike on the inside of the penultinate joint directed downward and backward, and a curved chitinous projection on the outside, as in the second leg. A few other setæ on the legs.

The *ventral surface* shows a median chitinous ridge, or sternum, with four transverse ridges or apodemata running to the epimera of the legs, and forming the skeleton. These divide the body into eight spaces, each of which bears two or more clear spikes.

The penis is long and straight, and is seen in the median line below the shield-shaped plate.

Female (figs. 2, 3). Average length about '26 millim. Average breadth about '22 millim. Average length of legs-1st and 2nd pairs about '06 millim.; 3rd and 4th pairs about '08 millim.

Colour. Yellowish chitinous-brown, of medium tint. The white excretory organs show through the dorsal surface, as in the male.

Texture. Chitinous, hard, and polished, particularly the anterior part of the carapace, which is slightly transparent.

General form oval, but so short and broad as to be nearly circular. This form varies a little, not only in different specimens, but in the same, according to the action of the muscles, the lateral parts of the carapace being slightly flexible.

The whole of the anterior part of the body is covered by a semilunar buckler, greatly resembling that of *Limulus*. This buckler projects far beyond the body both anteriorly and laterally, and extends as far back as the insertion of the 4th (posterior) pair of legs. The three anterior pairs of legs are entirely covered by this buckler when the creature is at rest, and almost covered by it at other times. The portion of the body posterior to the insertion of the 4th pair of legs is also covered by a projecting carapace; but this, instead of being fused into one mass, is clearly divided into three segments.

Cephalothorax. Small, much more distinctly divided from the abdomen than in the male. Rostrum shorter, broader, and more chitinous than in the male; it is usually carried folded down against the ventral surface. The mouth-organs, which are difficult to make out, appear less rudimentary than those of the male. The anterior pair of rod-like projections have become more substantial organs.

The abdomen, although much smaller than the carapace, is large in proportion to the cephalothorax; it approaches the circular form, but on the ventral surface bears a thin, colourless, shieldshaped plate, more plainly seen at its anterior than its posterior limit, the anterior angles projecting and covering the insertion of the third pair of legs.

There are two rows of colourless spines on the dorsal surface of the carapace, which may stand upright or lie backward; a few similar spines nearer the edge, and two smaller pairs near the posterior margin. There is a sternum, apodemata, and epimera, forming a skeleton on the ventral surface, as in the male.

Legs. The first two pairs rather the shortest, the first pair thicker than any other (except the basal joint of the fourth). The first leg (fig. 6) has the tarsus and penultimate joint fused into one considerably enlarged mass, as in Pyqmephorus, terminating anteriorly in a clear, chitinous projection, which carries an extremely large, sharply-bent, monodactyle claw, without sucker or caruncle. The enlarged terminal joint has a thinner ridge on its upper surface, bearing two very long hairs or spines, with two laurel-leaf-shaped pieces and a short spike between them. There are two strong curved hairs on the underside of this joint, and a few similar on the other joints. The second and third pairs of legs have the tarsus terminated by a didactyle claw, with a small caruncle between the ungues. These legs are abundantly haired, but there is not any hair which attains special prominence. The fourth pair of legs (fig. 9) have the first (basal) joint very thick and long; the other joints diminish in size regularly and rapidly. The tarsus does not bear any claw or caruncle, but terminates in two extremely long and powerful setæ, of which one is straight and the other curves towards it; the same joint bears three other curved setæ, which are smaller, but still large, and there are one or two setse on the other joints.

The whole body is attached to the dorsal carapace by a membrane, which covers the ventral surface and lines all parts of the carapace.

The alimentary canal shows plainly from the dorsal aspect. It consists of a long œsophagus, forming a slight ingluvies at the posterior end; a valve divides this from an almost globular ventriculus, from the posterior end of which proceeds the hind gut, very obscure, and almost entirely or quite hidden by the opaquewhite excretory organs which overlie it. From these last-named organs a straight median passage may easily be traced to the anus, which lies at the posterior edge of the carapace (ventral surface).

From the ventral aspect a main tracheal trunk may be seen on each side, proceeding from the rostrum and running nearly straight backward below the alimentary canal, and there are important tracheæ supplying the legs &c.

All the internal organization can be seen much more plainly in the female than in the male.

Larva.

Colourless, semitransparent. Texture smooth, almost polished. General form elliptical, margin lobed. The creature shows

segmentation very clearly. Rostrum oblong, almost square, hardly seen from above, being much folded down on the ventral surface; it is also very retractile, capable of being almost entirely withdrawn into the camerostomum; it bears two pairs of short setæ, but these do not spring from a tube as in Hypopus. There are a few smaller hairs. The dorsum is nearly covered by three transparent chitinous plates, slightly imbricated; they do not reach the lateral margin, and are rounded towards it. The first plate bears two pairs of large serrated spines slightly curved. each of the other plates bears one pair. There are two smaller similar plates on each side, each plate bearing a similar spine. Beyond these plates the margin is membranous; this part is wide posteriorly, and divided into large lobes all round. The posterior termination of the abdomen is a retractile lobe or segment, bearing two pairs of very long curved spines, of unequal length, the shorter being the thicker and most strongly serrated.

The legs are about half the length of the body, approaching conical, almost straight; coxæ thick; joints gradually diminishing; tarsi slightly curved when seen from the side; from that view they end very bluntly, and all three pairs are terminated by a strong didactyle claw on a slender peduncle. Two very long flexible setæ are inserted near the distal end of the first tarsus, shorter ones on the other legs; all the joints have several shorter spines. The creature is very mobile, and can lengthen and shorten its form considerably.

The egg is almost globular, milky-white, and without any conspicuous markings.

DESCRIPTION OF PLATE XV.

DISPARIPES BOMBI.

Fig. 1. Larva. Dorsal view, $\times 400$.

- 2. Adult male. Dorsal view, \times 200.
- 3. Adult female. Dorsal view, $\times 150$.
- 4. Adult female. Ventral view, \times 150.
- 5. Tarsus of first leg of male, side view, \times 600.
- 6. First leg of adult female, \times 800.
- 7. Claw of same leg (from within).
- 8. Ungues and caruncle of second leg of adult female.
- 9. Fourth leg of adult female, \times 500.

